XXV.—*On the Mechanism of Aquatic Respiration and on the Structure of the Organs of Breathing in Invertebrate Animals.*

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[With a Plate.]

The mechanism of breathing in the countless hosts of invertebrate animals which people the ocean, offers a problem which has never yet been satisfactorily solved. The mode in which life is sustained in those degraded forms, in which "a circulation of blood" is not to be discovered, has long stimulated the curious wonder of the naturalist. Fishes and Cetacea excepted, the invertebrate animals constitute the entire population of the ocean. Insects excepted, all invertebrate animals are aquatic. Hence the wide range of interest which belongs to this subject. How animals breathe is not second in importance to the question how they live. Every observer studies the latter, few the former. There are "habits" associated with the manner in which the function of breathing is performed which are well-fitted to win admiration. Wanting the knowledge of this process, not the smaller half of the history of an animal remains to be acquired.

It is the aim of this memoir to demonstrate first the anatomical conditions under which the office of respiration is performed in the invertebrate animals, and then to study the process itself. The anatomical conditions will prove as various as the classes of which this subkingdom is composed. Two primary divisions of this subject demand at once to be recognised; —1st, that comprising those organs which adapt the animal for atmospheric breathing; 2nd, that qualifying it to respire in water. The latter, embracing varieties more striking and numerous than the former division, should again be resolved into two denominations, of which one would comprehend the mechanism of those organs by which the *chylaqueous fluid* is submitted to the agency of the aërating element, and the other, that of those fitted to expose the true blood*.

All vertebrated animals, fishes excepted, breathe on the atmospheric plan. All invertebrate animals, insects excepted, respire on the aquatic model. The organs used in the first method are more complex than those comprised in the second; while the chylaqueous fluid is subjected to respiration, through the *least* complexly arranged mechanisms. The simpler the fluid to be

* The author would here beg to refer the reader, for a full statement of the grounds of this latter subdivision, to his paper on the Blood-proper and Chylaqueous Fluid, &c., in the Phil. Trans., Nov. 1852.

aërated, the less involved is the disposition of the solid parts through which the exposure is effected. Elaborately vitalized blood is circulated through respiratory organs of inconceivable complexity and subdivision. The study of the mechanical conditions of respiration should regard the *fluids* as well as the *solids* of the structures dedicated to this function. The floating cells of the fluids are concerned in, though not essential to the respiratory process. The *true capillary segments* of the lungs of *all* vertebrated animals, those of reptiles *not* excepted, are destitute of vibratile cilia. The branchiæ of fishes, without a single known exception, are clad only by a *non*-vibratile epithelium. The general proposition, that ciliary epithelium constitutes no part of the *active portions* of the breathing organs of vertebrated animals, rests therefore upon the stable basis of actual demonstration. This negative must be changed into an affirmative statement, with reference to the air-*passages*, which in the pulmonary vertebrated series are profusely and universally ciliated. The presence of cilia on the branchial structures of invertebrated animals is a common, but not a constant fact; the rule without intelligible reason is suspended in numerous instances. The operation of cilia is therefore *not* indispensable to the respiratory process, even in the invertebrate animal—not an *essential* constituent even of the aquatic model. The blood of all vertebrated animals is richly charged with corpuscular elements. It is invariably coloured red. In the invertebrated subkingdom not one example is known of a corpusculated *red*-blood. The blood of every known mollusc bears floating solid elements. In every articulated animal the true-blood abounds in organized corpuscles. In every annelid, without a single known exception, the blood-proper is perfectly destitute of morphotic elements; it contains no trace of visible cells. The perfect fluidity of the true-blood of all Entozoa can also now be affirmed. Every Echinoderm is endowed with an imperfect blood-system, the blood-proper bearing cells in suspension. The chylaqueous fluid of every animal in which it exists, is charged more or less abundantly with organized corpuscles. The generalization is thus incontrovertibly established, that there exists no single instance of a real animal, of which one or other of the circulating nutritive fluids of the organism, is not replete with morphous particles. What office, if any, these floating solids exercise in the *mechanism* of the respiratory act, it is the province of the physiologist to determine; their microscopic characters it is the duty of the anatomist to describe.

Porifera.—In the Spongiadæ, the fluids to be aërated are contained *in* and *between* the component cells of the gelatinous cortex. Each separate cell, like that of *Amœba,* is an independent organism. The included fluid, moved by the slow contraction of the cell-membrane, is a granulated, nutritive compound. That diffused between the cells, in composition, is less removed from the standard of sea-water. The latter replenishes the former. The inorganic fluid, entering from without into the interior of the living-cell-tissue, carries with it in solution a large amount of atmospheric air. In these lowly organisms, this dissolved air probably suffices to *oxygenize* their simple fluids. As the contained fluids are rapidly renewed, the nutritive and the respiratory process come to be performed by one and the same act. This is the history of the breathing function in the *Rhizopoda* and in *Actinophrys Sol*, recently described by Kölliker*. The superficies of the whole gelatinous cortex of the sponge is overspread by a film of ciliated epithelium. It has now been proved by Dr. Dobie† and Mr. Bowerbank, that the "currents" of the sponge are due to the agency of these motive organules. These currents are simultaneously nutritive and respiratory.

Polypifera.—Three varieties of plan, in the mechanical conditions of respiration, prevail among Zoophytes: the *Hydraform* (Pl. XII. fig. 2), the *Actiniform* (fig. 3), and the *Asteroid polypes* (fig. 1) exemplify three minor forms of one type of structure. In the first the space between the stomach and the outer limit of the body (fig. 2, *a*) is subdivided by the intersection of delicate tissue into areolæ, in which the fluid to be aërated is contained ‡.

The fluid penetrates along an axial channel to the furthest

* See Quarterly Journal of Microscopic Science, Oct. 1852.

† See Annals of Anatomy and Physiology, No. 2, May 1852.

‡ The author has stated in the text the impression which he has derived from numerous observations on the common hydra of our pools, that the tentacles open into the *perigastric* areolæ, as shown at (*a*) fig. 2, and not into the stomach, and that they are *tubular*, not solid threads, as shown at (*b*) fig. 1. If, as recently stated by Prof. Allman (Proceedings of the Royal Society, May 31st, 1853), they open directly into the stomach, the tentacles can only be injected by the contents of the latter, and their function would partake of a digestive as well as a respiratory character; and further, the digestive system of the hydra would conform with the medusan type which is marked by the direct extension of canals from the stomach, and by the absence of a splanchnic cavity, the stomach being merely an excavation in the solid parenchyma of the body. The observations of Prof. Allman were instituted on *Cordylophora*, a genus of *Tubulariadæ*. According to my researches very lately made on *Tubularia indivisa* and *Alcyonium*, the tentacles are tubular and open into the perigastric chambers, which they equal in number. From its interest, this question cannot remain long unanswered. If in the hydraform and tubularian zoophytes the tentacles are prolongations of the stomach, properly so called, zoophytes, as a class, might be ranged under two leading divisions; that 1st in which the tentacles are *gastric*, and 2nd that in which they are *perigastric* prolongations. The *fluids* would admit of a similar division.

ends of the tentacles: they are *not* perforated at their distal extremities. In *Hydra viridis* and *H. fusca*, by means of the rolling granules, the fluid may be readily detected by the eye. It cannot be renewed *directly* from without. It is replenished *through* the walls of the stomach (*b*). The respiratory is here a function distinct and separate from the digestive. A living corpusculated fluid is submitted to the influence of the surrounding medium, by aid of the tentacles. These appendages in the hydraform zoophytes are furnished neither within nor without with motive cilia. They maintain the flux and reflux motion of the embraced fluid, in virtue of the contractile endowments of their parietes. In the *second* variety, illustrated by the sea-anemone (fig. 3, *b*), the open interval between the stomach and the integuments, though partitioned by dissepiments, is very capacious. The hollow axes (*c*) of the tentacles are continuations, in all species, of the perigastric space. They are filled with the same fluid as the latter. In some species of *Actiniæ*, the tentacles are perforated at the extreme ends: *Anthea Cereus* is an example. In the greater number they are cæcal. The *interior* of the tentacles, in common with the perigastric chambers, in *all* species are richly ciliated (*d*). The exterior of these appendages in many instances is covered only by an ordinary non-vibratile epidermis. The chylaqueous fluid* is an inferiorly vitalized

* Under this term (see Phil. Trans. 1852), the author has ventured to distinguish the fluid which occupies the gastric and perigastric cavities of *all* animals below the Annelida. He has elsewhere endeavoured to prove the proposition, that in all animals *below* the Echinoderms, it constitutes the *exclusive* nutritive fluid of the organism; that in those families, as in Zoophytes and inferior Echinoderms, in which it is readily ejected from the body and as readily replaced, it is very little removed in composition from salt water, and corpusculated only in a slight degree. It is simply albuminized sea water. But it has already undergone such preparation as fits it to enter the "protean" cells of the solids. Here, as illustrated in the examples of the *Amœba* and Sponge, it assumes a more highly vitalized and corpusculated character. It may be said that in the cells it is true blood, in the visceral cavity chylaqueous fluid. The difficult problem of respiration in the lowest forms of animal life can be solved *only* by determining the real stages through which the fluids pass in the processes of animalization. If the great mass of the chylaqueous fluid contained in the polypedal and visceral chambers consist of pure, unvitalized, unalbuminized sea water, *then* the tentacles can subserve no respiratory purpose; since between two fluids (that within, and the element without the tentacles), of identical composition and specific gravity, there can occur no interchange of gases. But if, on the contrary, to this great reservoir of fluid be assigned the value of a chylaqueous compound, though it may have undergone only the first and lowest grade of assimilation, *then* the entire mechanism of respiration and nutrition becomes intelligible. This argument enforces the physiological principle, which, in order to demonstrate the true seat of the aërating process, demands that the real constitution of the fluids be *first* discovered. In studying the nutritive and respiratory actions in *all* invertebrate animals,

albuminous compound. It possesses higher organic properties in those orders in which the tentacles are closed, than in those in which they are open. In the former it sojourns longer in the visceral cavity under the influence of the Zoochemical forces. It is in the interior of the cells of the solid structures that the chylaqueous fluid acquires its final properties. It suffers here a second and higher nutritive and respiratory change, or derives from the chylaqueous mass, still in the visceral cavity, a further supply of oxygen. The chylaqueous fluid is aërated in two modes; 1st, every portion of the element from without, which is admitted into the splanchnic cavity, brings with it a fresh supply of highly oxygenized air; and 2nd, it exchanges its carbonic acid for the oxygen of the surrounding element, in accordance with the principles of ordinary aquatic breathing. It is therefore a reservoir of richly oxygenated fluid, fitted well to impart a renewed proportion of oxygen to the more highly vitalized contents of the cells. It is evident that it is only by a clear statement of these *apparently* irrelevant particulars, that the anatomist can arm the physiologist with an adequate conception of the *physical conditions*, under which the respiratory function occurs in these degraded organisms. In all actiniform polypes, the bottom of the stomach communicates, by means of a sphincteric aperture, with the perigastric chambers. It is by this route that the large mass of the contents of these latter cavities are derived from without. The contained fluid receives the first impress of the vital chemistry, in its passage over the gastric surfaces. It is then prepared to undergo the respiratory changes in the visceral cavities. The preceding observations apply to the *third* (fig. 1) variety of plan (exemplified in the *Asteroid* families), on which in zoophytes the fluids are elaborated. There is little difference of structure between the asteroid and helianthoid polypes. In the former the stomach is prolonged into the axis of the polypidom (*c*). The perigastric chambers (*d*) also communicate, but in a less direct

one fact of singular interest should be remembered, the truth of which the author has established by numerous observations. The *cells* of the solid tissues are *contractile*; they *contract* and *dilate*: in the Cephalopods, the pigmented cells of the integumentary structures exhibit this property with remarkable distinctness. The pigment is deposited in the substance of the cell-wall. When the cell *contracts* the coloured point disappears, when it expands it assumes a conspicuous area. This is the simple explanation of the singular power, with which the Cephalopods are gifted, of *changing their colour*. It applies also to the chameleon. But in invertebrate animals it is not confined to the pigmented cells. It is exhibited by the non-pigmented cells of nearly all the structures of the body. The author has ventured in this place to bring it under the attention of the physiologist, because it is unquestionably a property of great importance in the circulation and aëration of the fluids.

manner than the stomach, with the channel of the stem. In these families, the tentacles, which are evidently the continuations of the perigastric chambers (fig. 1, *a*), are said to be perforate at their distal extremities: this point requires to be confirmed. The fluid filling the axial channel of the stem enters at the mouth of each polype, and descends through the orifice situated at the base of the stomach (fig. 1, *c*) into the polypidom. In this situation, in a great variety of species, the motion of the corpuscles contained in the fluid may be readily observed. They present all the characters of being driven by *cilia*. The presence of cilia is however controverted by some observers. From the polypidom the fluid passes upwards into the perigastric chambers, and thence into the tentacles in which it undergoes aëration. It is curious that the *corpuscles* of the fluid of the stem do *not* pass upwards into the tentacles. They are filtered back by the cribriform partition, which divides the chambers around the stomach from the axis of the polypidom. *New* observations are required on the whole family of the asteroid polypes, having special reference, 1st, to the arrangement and existence of cilia, and 2nd, to the distribution of the fluids.

The fluid by which the whole extent of the stem and visceral chambers of each individual polype are distended, constitutes one system. So rapidly is this fluid endowed with a low order of vital properties, enabling it to fulfil its functions as an element of nutrition, that it may be rejected *en masse*, to be replaced with a fresh volume of *in*organic water. Such is the converting power of the vital chemistry in these simple organisms. This fact distinguishes the polype families from all other invertebrate animals. The true character of the breathing function must have remained beyond the reach of the physiologist, without the knowledge of these points. They prove that the *lower* the vital endowments of the fluids, the simpler the mechanical arrangements required to effect their aëration. In zoophytes the nutritive fluid is not exclusively vitalized through the agency of floating cells, it is vivified in part, catalytically by *contact* with the surfaces of the living solids. The morphotic elements, therefore, which exist in the fluids of this group, are scanty in number, subordinate in function, and indeterminately organized. To detect the globules in the fluid of the polypary is easy. It is more difficult to trace its progress upwards into the space which surrounds the stomach, and thence into the tentacles. If, as lately stated by Prof. Allman*, the axes of the tentacles in the tubularian polypes open directly *into the stomach*, and *not* into the space to the outside of this organ, these appendages cannot be intended to expose the

* Proceedings of the Royal Society, May 31, 1853.

chylaqueous fluid to the aërating medium. Arising out of the roof of the stomach, as already stated, at the side of the oral orifice, they can be injected only with the contents of the stomach, and that periodically by muscular force. Such a mechanism, for organs which are indubitably respiratory, is in the highest degree improbable. The tentacles of the distended polype are filled undoubtedly by a *fluid*. In *this* fluid no corpuscles have yet been detected. Those observed so readily in the stem cannot be traced upwards beyond the base of the stomach : Prof. Allman denies even in the latter situation the existence of cilia. The globules move, according to this observer, as "the effect of the active processes, going on in the secreting cells of the endoderm, —processes which can scarcely be imagined to take place without causing *local* alterations in the chemical constitution of the surrounding fluid and consequent disturbance of its stability." However these questions may eventually be determined, it is certain that there exists in all zoophytes but *one fluid system*.

This fluid is compounded of the surrounding medium, whether it be sea water or fresh, and the organic products of digestion. By this quasi-inorganic fluid the nutritive functions of the organism are performed. In the tentacles it undergoes aëration; in the actiniform orders it may be collected in large quantities: it contains corpuscles characteristic of species*. It affords distinct evidence of the presence of albumen; it is destitute of fibrine; it is the lowest example under which a living nutritive fluid occurs in the animal kingdom, and yet *the cells of the solids* of zoophytes are eminently irritable and contractile. An inverse proportion obtains generally in this respect in invertebrate animals. The simpler the fluids, the more irritable and contractile the solids, the cells of the latter being larger than the corresponding parts of vertebrated animals.

Bryozoa (fig. 4).—The marine and freshwater polyzoa are molluscan in the character of their alimentary system, zoophytic in that of the fluids. Their position in the scale must be allotted according to the relative importance of these two systems: judged by the fluids, they claim to rank at the summit of the zoophytic series; by the alimentary organs, they would constitute the first link in the molluscan chain. The real signification of the fluids in the Polyzoa has never been understood. A perigastric cavity (*a, b*) is clearly described; the *fluid* within this cavity and its floating corpuscles have been repeatedly observed, but the physiological value of these parts has never been explained†. In these

* See the author's papers on the Blood, which are now in course of publication in the British and Foreign Med. Ch. Rev.

† In justification of the statements made in the text, the author would refer to the admirable report, on the Polyzoa, by Prof. Allman, in the Trans.

animals there exists neither a heart nor a blood-proper system. The fluids constitute an unmixed example of the chylaqueous system. They oscillate under muscular agency in the great visceral cavity (*a,b*); under the same force the fluid penetrates the tentacles which it traverses by a flux and reflux motion. These organs are plain, tubular appendages; they are continuations of the visceral cavity; —characters which are emphatically zoophytic. The tentacles of the Polyzoa differ from those of asteroid polypes in the presence of vibratile cilia. They are limited to the external surface, and arranged in a single row on either side: the interior of these branchial tubuli is not ciliated. Thus then is defined the whole apparatus of the chylaqueous system in this family. Henceforth the Polyzoa cannot be severed from the zoophytes.

Acalephæ (figs. 5, 6, 7).—The apparatus for breathing is, in this class, of simple construction: it consists of a system of cæcal canals in direct connection with the stomach. Four types occur —the Pulmograde, the Ciliograde, the Cirrhigrade, and the Physograde. In the first examples (*Aurelia, Pelagia, Chrysaora, Rhizostoma, Cassiopea* and *Cyanæa*), the stomach is a central lobulated chamber, furnished with one external orifice, the mouth, and opening laterally into canals which reticulate at the margin of the disc: they end cæcally. In *Cyanæa aurita*, they are prolonged *into* the fringed appendages which depend from the cir-

of the Brit. Assoc., 1850, in which the following statements occur. "The perigastric space and interior of the tentacula and locophore all freely communicate with one another, and are filled with a clear fluid, in which float numerous irregular particles of very irregular form and size......That the fluid thus contained in the perigastric space, and thence admitted into the tentacles, consists really of water which had obtained entrance from without, there can, I think, be little doubt; and yet I have in vain sought for any opening through which the external fluid can obtain admittance into the interior......The fluid which circulates in the perigastric space is not perfectly homogeneous, and numerous corpuscles of various and irregular shape may be observed to float through it and be carried about by its current. Some of these corpuscles are perhaps spermatozoa; others are of no definite shape, and look like minute portions of the tissues separated by laceration. May they not be some of the products of digestion, which have transuded through the walls of the alimentary canal, being thus conveyed into the *only* representative of a true circulation, with which these animals present us?" From the preceding passages it is undeniable that this excellent naturalist has not clearly seized the significance of that which he has described so graphically. He admits that the fluid of the perigastric cavity is the *only* fluid system discoverable in the organism of the polyzoon. He disputes the organic character of the fluid, while he *hints* at its nutritive properties. It is in truth a true and perfect *chylaqueous system,* and as adequate as blood-proper to the wants of the living organism. In the Polyzoa, there is discoverable no trace of a blood-proper system. They therefore *fail* in one of the most essential characters of the molluscan organism—the existence of a heart and an associated circulatory system.

cumference of the disc. The system of the gastro-vascular canals (fig. 5, *c, d*; fig. 6, *c, d*; fig. 7, *c, d*) in the *Discophoræ*, forming a horizontal plane, rest in immediate contact with the *inferior* surface of the disc—that is, the whole substance of the disc intervenes between them and the *upper* surface: the under surface of the disc externally, in every species, is ciliated; the superior is not so. The stomach *and the canals* (*c, d*) to their remotest terminations are ciliated *internally*. This fact distinguishes these canals fundamentally from blood vessels; they are filled with a fluid which is imperfectly vitalized, a chylaqueous compound; it is replete with floating organized corpuscles. The flux and reflux motions of this fluid are excited, partly by cilia, and partly by the rhythmic contractions of the disc. Respiration is accomplished in two modes; partly by the interchange of gases on the under surface between the contents of the canals and the surrounding element, and partly by the air suspended in the external fluid, which is admitted through the mouth and stomach into the gastro-vascular channels directly from without.

The basis and bulk of this fluid is composed of salt water, but qualified by the impresses of the zoochemical influence to sustain the *life* of albumen, fibrine, and to evolve definitively organized floating corpuscles. The refuse portions of this fluid are rejected *per os*; there is no anal outlet. The cells of the solid structures of the Acaleph are filled with a semifluid hyaline jelly; it is the chylaqueous fluid in its highest grade of organization. In the Medusa, it is to the chylaqucous fluid, what the contents of the "protean" cells of the gelatinous cortex are to the currents of the circumambient element, traversing the passages in the sponge: thus, in brief, is conveyed a description of the *machinery* of the respiratory process in the Acaleph; from it the nutritive processes cannot be distinguished. The *Ciliograde* family departs from the type of the former in one particular; there exists here a *second* orifice to the digestive system (fig. 7, *b*). The fact alters not the principle of the mechanism, according to which the fluids are aërated. The gastro-vascular canals arise from the fundus of the stomach, attain the surface, and pass in meridional series (fig. 7, *c, d*) from one pole of the body to the opposite, lying immediately underneath the external epidermis. Their courses are followed externally by rows of motive cilia, or vibratory fringes: all the canals peripherally terminate cæcally; they are furnished on *their internal* surfaces with cilia. The genera *Cydippe, Cestrum* and *Callianira* are illustrative.

In the *Cirrhigrade Acalephs*, the second orifice of the alimentary apparatus disappears. The canals, filled with the chylaqueous fluid, radiate, while they multiply in the direction of the circumference of the disc. Like those of the preceding families, they are ciliated internally, while they are distributed in close proximity to the under surface of the dome.

The organization of the *Physograde Medusæ* is little understood*.

It cannot be doubted, that in the *fluids* of the Acalephs, floating corpuscles, from their multitude and their determinate structure, exercise an important part. They animalize the fluid; they endow it with life. Directly or indirectly they develope the proximate principles out of the inorganic elements. Both the corpuscles and the fluid contained in the gastro-vascular canals are nearly colourless. Here, as in many other instances amongst the invertebrate animals, the lesson is taught, that *colour* has little to do with the capability of vital fluids to absorb oxygen. In this class, it is beyond question, that sea water is admitted directly into those canals in which the chylaqueous fluid is contained. The former is so rapidly assimilated with the latter, that the nutritive and vital character of the compound fluid resulting from the admixture is readily maintained at the required standard.

It is important to remark, that in all Acalephs the gastro-vascular canals are distributed as closely as possible to some *external* surface; in *Rhizostoma* to the under surface of the dome, in *Beroë* in meridional lines over the globe, in other species along the margins, &c. Such disposition has reference to the respiratory process: vibratile cilia in general are developed on those portions of the external surface which coincide with the gastro-vascular canals.

Echinodermata.—In this class the same questions arise, as important preliminaries to the study of the respiratory process, with those as to the *meaning of the fluids*, which were discussed with reference to the inferior Radiata;—which of the *three* orders of fluids, present in the œconomy of nearly every Echinoderm, is made the *special* subject of this process? 1st, the cavity of the body (figs. 8, 9, *d*; fig. 10, *n*) (*i. e.* the spacious interval which separates the digestive from the integumentary system) is filled in *all* species with a fluid which the author has called the *chylaqueous*: 2nd, the protrusile suctorial feet (Pl. XII. fig. 8, *g*; fig. 9, *f*) are occupied by another class of fluid; this system constitutes the water-vascular system of Tiedemann and Müller; 3rd, the blood-vascular system (fig. 10, *j*), of Tiedemann, Delle Chiaje, Valentin, Agassiz, Dr. Sharpey and Müller: these three systems are defined as severally distinct and independent, and

* See a paper in the Ann. des Sc. Nat. tom. xviii. "Sur la Structure des Physalies et des Siphonophores," by Leuckart.

their functions respectively are alleged to be distinct and independent. In what conceivable manner is the descriptive anatomist to depict the breathing systems of these animals, unless by that of first adjusting these long-controverted questions? The ultimate structure of those solid parts, on which the office of aërating the vital fluids is represented to devolve, must be first determined. This inquiry alone can prove to what extent, if at all, these parts are capable of answering the purpose which they are stated to fulfil. The chylaqueous system of fluids exists in *every* Echinoderm; the water-vascular system does *not* exist in every species. In the *Sipuncles* and the *Ophiuridæ*, it has no place. The blood-vascular system is very imperfectly known. Little has been done to demonstrate its presence in the asteroid Echinoderms, and still less in the Echinidæ. Its history has been most fully developed in the Holothuridan and Sipunculidan genera.

1. *The Chylaqueous System of the Echinoderms.*

Is it capable of subserving a respiratory purpose? Is it constituted such that it is physiologically capable of executing this great function? And is it also *distributed* appropriately?

The mass of fluid occupying the visceral cavity, bounded on one side by the digestive system, on the other by the integuments, has been described, by the classical authorities upon this subject, as consisting purely of sea water, admitted *directly* from without through the skin, for the exclusive purpose of aërating the blood-proper, said to circulate in a *capillary* system of vessels wrought in the solid parietes circumscribing the cavity. This, in succinct expression, is the doctrine of the schools, as to the mechanism of respiration in this interesting class of animals. It supposes the existence of a profuse plexus of capillary vessels carrying true-blood, distributed over *all* the visceral and parietal surfaces limiting the chamber in question. It may be at once stated, that no approach to a demonstration of the presence of this system has ever been made by *any* modern or ancient anatomist. Is it logical to erect one hypothesis upon another? Let *facts* be first represented. In the Asteridæ, Echinidæ, Ophiuridæ and Ophiocomidæ, the fluid contained in the peritoneal cavity has been described by every comparative anatomist as pure unmixed sea water. It cannot be denied that the cavity itself is the anatomical homologue of the real perigastric chamber of zoophytes and of the gastro-vascular canals of Medusæ. It is therefore the anatomical *locale*, in which the chylaqueous fluid *should* accumulate; but under what character does it occur in the higher vermiform Echinoderms? In the Holothuridan and Sipunculidan genera (fig. 10, *n*), it presents itself as a chamber filled with a chylaqueous compound, under the unquestionable form of a thickly corpusculated milky fluid, organized in a high degree, and oscillating as a living nutritive fluid: it is by tracking the characters of this fluid from above downwards, that its real signification in the inferior Echinoderms, in which it offers the *apparent* properties of simple sea water, can be unerringly ascertained. The floating corpuscles of the chylaqueous fluid of the Sipuncles (fig. 10, *h*) present the features of *constancy* in structure and proportion; they are always the same in the same species. The cephalic appendages in this genus, as well as the whole integumentary system of the body, are organized with express reference to the exposure of *this fluid*, and this fluid exclusively, to the agency of the external aërating element.

The skin is *fenestrated* (fig. 11, *d, d, d*), that is at regular intervals the muscular layer disappears, and an interval of elliptical figure, covered over only by a single layer of epidermis, results. In the *solid* structures of the integuments there is no trace whatever of a capillary vascular system to be detected. It is a simple membrano-muscular partition, intervening between the chylaqueous fluid within and the surrounding element without: it is *through* this veil that these two divided fluids interchange their dissolved gases. The tentacles present the same precise mechanism (Pl. XII. fig. 10, *a* & *C*, & *B*); they are merely hollow appendages, musculo-membranous, lined *within* and *without* by a ciliated epithelium. A *few* proper blood vessels reach their bases from the circular vessel; but *no* trace whatever of a vascular plexus, in the *structure* of these parts, can by any manœuvre be discovered. The inference is irresistible, that, like the skin of every part of the body, which *internally* is universally ciliated, the tentacles are designed almost exclusively as instruments for the oxygenation of the chylaqueous fluid (*not* the blood proper), which oscillates by a flux and reflux movement in their hollow interior. To the genus *Holothuria* these observations in every detail are strictly applicable. The tentacles, however, though hollow membranous appendages, are furnished, *in the substance of their parietes,* with a few more blood-vessels: the skin is fenestrated like that of the Sipuncles (fig. 11); the open cavity of the body is occupied by a highly organized corpusculated fluid which the solid parts just described are expressly fitted to aërate. From its volume, its organic composition and its suspended cells, its importance in the organism cannot be disputed. It cannot acquire nutritive properties unless through the agency of oxygen. This element can be received through no other provisions than those exhibited by the skin and the tentacles: thus the *theory* of respiration, with respect to the chylaqueous fluid, in these superior Echinoderms is complete. Although attenuated at regular points, with a view to approximate as closely as possible the chylaqueous fluid to the external medium, no *open perforation anywhere* exists in the tentacular or integumentary processes. The surrounding fluid cannot therefore penetrate *directly* from without into the peritoneal cavity*. It is introduced through the mouth and the digestive system.

In the *Ophiuridæ* and *Ophiocomidæ*, the visceral cavity is filled with a fluid, which, though not so highly organized as that of the preceding genera, is undoubtedly the same system: it is not so milky in appearance; it approaches more to that of pure salt-water. Its floating corpuscles are far less abundant, and more indefinitely formed; its oscillations are ceaseless under the movements of the arms and action of cilia. At the flexures of the articulated pieces of the arms, soft, membranous, hollow processes, opening into the peritoneal cavity, protrude.

They are designed to aërate the fluid contents of the visceral chamber: unlike the membranous integumentary projections of the Asteridæ, they are neither ciliated within nor without. They may be seen perfectly in the smaller species, as transparent objects. If any vestige of a blood-proper system of vessels occupied the substance of their parietes, it could not, thus examined, escape detection; none such exists. Wherefore then are these specific organs provided, if not to arterialize the great system of fluid which penetrates into their interior? The answer cannot be withheld; it is to aërate the chylaqueous fluid exclusively†. The chylaqueous system of the Echinidæ (fig. 9), comprehending a considerable mass of fluid filling the cavity of the spherical shell (*d*), has never yet been recognised by the anatomist as a vital organic system. The great authorities, Agassiz especially, formerly quoted, state that sea water streams into the visceral cavity through perforations in the membranous processes (fig. 9, *f*, *f*) of the shell, especially in those under the name of *branchiæ*, which are distributed in groups around the circumference of the oral membranous disc. The latter are *not* connected with the suctorial or water-vascular system; they are distended by injections thrown into the open chamber of the shell.

They are protruded only by the force of the fluid driven into their interior. They collapse by contractility of their parietal

* The author would again refer the reader to his recent memoir in the Phil. Trans. (1852), for a full and complete statement of the anatomical and experimental evidence, by which are substantiated the general propositions enounced in the text.

† It will be afterwards shown, that comparative anatomy has done absolutely nothing towards the demonstration of the blood system of these Echinoderms. A circular vessel is stated by Müller only to surround the mouth.

structures. They are *not perforated* at their extremities (*b*). They *cannot* therefore serve as open passages for the direct admission of the external medium into the visceral cavity. They are unquestionably in part tactile appendages. In addition to the meridional rows of suctorial feet, the shell of *Echinus* is perforated by numerous hollow membranous processes (fig. 9, *f, f, f*), lined within and without by vibratile cilia, and *penetrated* exclusively by the fluid of the visceral cavity. Like the integumentary structures of the higher genera, they bear no evidence whatever of blood-vessels. These facts impel the physiologist to the adoption of one inference. They *can* only subserve a respiratory purpose on the supposition that the *subject* of that process is the chylaqueous fluid. *Then* the conclusion cannot be evaded, that, although in the *Echinidæ* the fluid contained in the visceral cavity may *look* like simple sea water, it must be something more; else *nothing* would be signified by the express provisions supplied, to subject it to the process of aëration. It is, in truth a dilute albuminous solution, charged with corpuscles indeterminately organized. It possesses a higher solvent power for oxygen than simple sea water. It is the reservoir out of which the elements of the true blood are drawn. Injection thrown into the hollow of the shell of *Echinus* distends beautifully, in relief, numerous membranous appendages belonging to the integumentary system. In *no instance whatever* can any *perforations* in the extremities of these processes be detected. There is therefore no direct evidence for the opinion commonly entertained by the best observers of the Echinoderms, which affirms that the external water enters immediately through openings in the *integuments* into the peritoneal cavity*.

The preceding questions admit of more easy and satisfactory solution in the Asteridæ than in the classes of Echinoderms already reviewed. *Asterias rubens* is a large animal; the fluid

* On the subject discussed in the text, Müller, in his recent elaborate essays on the Echinoderms, published in his 'Archiv,' offers the following remark, which I produce in the original:—"Die baumförmigen Kiemen der Seeigel, die äusseren Kiemen Valentin's sollen an den Enden ihrer Aeste nach Tiedemann offen sein, auch das Wasser in das Innere des Seeigels aufnehmen. Diese Ansicht gründet sich auf Injection mit Quecksilber unter gleichzeitiger Anwendung von gelindem Druck. Valentin fand diese Organe dagegen an den peripherischen Enden geschlossen, so dass sie also hohle Verlängerungen der Leibeshöhle nach aussen darstellen, und die Athemfunction auf ihrer äussern Oberfläche stattfindet. Auch ich habe bei wiederholter microskopischer Untersuchung dieser Theile von lebenden Seeigeln *keine* Oeffnungen an den abgerundeten Enden wahrgenommen." Müller, however, does not explain in what manner the "Athemfunction" of these appendages, which he argues to be cæcal, is possible. His conclusions as to the *imperforate* character of these parts I have repeatedly confirmed by variously devised methods of examination.

by which the visceral cavity (fig. 8, *h*) is filled is considerable in volume. The whole integumentary structures are more readily subjected to demonstration. Everything is favourable to a final conclusion of the controversy which has long divided anatomists as to the real signification of the fluid contained in the visceral cavity: it can be placed, in several modes, beyond doubt, that *no open perforations* exist *in any part* of the integumentary parietes of *Asterias*. The membranous processes (fig. 8, *f*, *f*) *openly* communicating with the visceral cavity are so remarkably elastic and protrusile, that, by means of coloured size forced carefully into the cavity, they distended to a great distance above the plane of the external surface. They are *cæcal* at their distal extremities.

This injection escapes externally only by rupture: this simple expedient proves the cæcal character of these parts; they are *not* consequently designed to admit sea water into the interior of the body. It is perfectly easy to repeat and confirm the first observation of Dr. Sharpey, that the corpuscles of the visceral fluid advance to the distal end of these processes, and then return under the impulse of ciliary agency*. Although an injection so thick as size will not escape through these membranous processes, a thinner fluid, such as coloured water, will slowly ooze through; it is not therefore improbable that an interchange of the fluids, which their attenuated parietes only divide, may *to some extent* occur through endosmose. This fact, however, cannot shake the stability of the conclusion, that anatomy does not furnish *any* grounds for the belief that the fluid contained in the peritoneal cavity is derived directly from *without*. The microscope renders it certain that the hollow membranous processes, filled by the fluid of the visceral cavity in *Asterias*, bear in the solid substance of their parietes no trace of true blood-vessels; they are lined within and without by vibratile epithelium, and composed only of interlacing elastic fibres. What conceivable office can such organs execute, if not that of exposing the chylaqueous fluid to the renovating influence of the surrounding medium? In *Asterias* this fluid approaches "simple sea water" closely in physical properties. It is, however, in reality a dilute albuminous, opalescent solution. It is charged scantily with

* Müller confirms the conclusions stated in the text—"Die respiratorischen Röhrchen auf dem Rücken der Asterien, welche mit der Bauchhöhle communiciren sollen zufolge der Injection von Tiedemann am Ende offen sein, und zum Wechsel des Wassers des Leibeshöhle dienen. Nach Ehrenberg dagegen sind die Röhrchen am Ende geschlossen, er sowohl als Sharpey sahen die Strömungen im Innern am Ende umkehren. An jungen lebenden Exemplaren des *Asteracanthion violaceus* sah ich dasselbe, und es gelang mir nicht eine Oeffnung wahrzunehmen."—Anatomische Studien über die Echinodermen. Müller's Archiv, 1850.

imperfectly formed corpuscles always the same in the same species.

In other species of Asteridæ the membranous appendages of the skin present other varieties in size and figure, none in character and structure.

In *Uraster papposa* the membranous intervals in the calcarcous trellis are large and favourable for examination. They may be readily seen with the naked eye in the living animal to be capable of being bulged out under the pressure of the fluid in the visceral chamber.

The Cribellidæ present another modification of the soft part of the integument. The skin is smoother, the membranous intervals are smaller, and the membranes are less capable of protrusion outwards. In every other respect they are identical with the corresponding parts of the preceding genera. The proposition may now then be finally affirmed, that in the Echinodermata the chylaqueous fluid (*i. e.* the contents of the visceral cavity) is *itself first* aërated, and that by means of a machinery of soft parts expressly arranged with a view to this end; and that then *it aërates the blood-proper.*

2. *Water-vascular and Blood-vascular Systems of the Echinoderms.*

To what extent, in what manner, if at all, do these two fluid-systems, or either of them, participate in the mechanism of the respiratory process? In solving the curious problem presented by the Echinodermal organism, the highest interest attaches to this question. Let it be first seen whether the statements of Tiedemann, Sharpey and Müller, that these systems are perfectly independent of each other and of the chylaqueous system already described, are really founded on trustworthy demonstration. No anatomist up to the present time has done more towards elucidating the anatomy of the true blood-system of the Echinoderms than that of proving the existence of certain central trunks *only*. This system has never been traced to its peripheric distribution *in any species* (the Holothuridan *perhaps* excepted) by any comparative anatomist. An induction is unsafe which is grounded upon hypothesis. The theory of respiration can only be constructed out of the materials supplied by the patient labours of the anatomist. It does not appear that Dr. Sharpey ever could verify the description of Tiedemann with reference to the blood-system. The tenuity of their coats however, and pale colour of their contents, render it extremely difficult to trace completely the distribution of the vessels*. Müller concurs in the description of Tiedemann, stating that in *Asterias* a circular trunk surrounds the mouth and gives off branches to each ray—

* Art. Echinodermata, by Dr. Sharpey.

adding the confession, that "*die Injection vom Blutgefässring gelang nur bis zum Anfang dieser Gefässe.*" And this is all that the author of this memoir has ever been able to accomplish to *prove* the existence only of the central trunks. This is the sum of the existing knowledge with reference to the blood-proper system of the Asteridæ. Of that of the Echinidæ very little also is known. Müller describes a circular vessel embracing the œsophagus immediately underneath the lantern; from this a trunk proceeds coursing along the curves of the intestine, and ending in the *circulus analis*. This learned anatomist observes, "*Um eine klare Vorstellung vom Herzen zu bekommen, muss man es bei* Cidaris *untersuchen; es ist bei* Cidaris *ein weiter, ganz gerader Canal mit dicken weichen Wänden* *." In *Cidaris* the heart is not a circular vessel, but a fusiform trunk lying parallel with the intestine. The *circumference* of the blood-system in the preceding genera has never yet been brought under demonstration. In science negative is inferior in value to positive proof; but at present it is only possible to declare that no care can succeed in discovering any evidence whatever of the presence of a blood-proper system in the solid structures of any part of the body of the Echinoderm. The parietes of the alimentary canal are *most certainly* not ramified by blood-vessels. The soft parts of the integumentary system are literally destitute of vascular tissue. The contents of the central trunks of the blood-system are identical in appearance with those of the visceral cavity, *and* with those of water-vascular or suctorial system; that is, when the morphous elements of these *three* fluids are placed in juxtaposition under the microscope, it is impossible to indicate between them any difference whatever in structure or shape. The fluids themselves are also identical in every physical appearance.

The *blood-vessels are internally and externally lined with cilia*, the water-vessels are so, and the visceral cavity is richly so. What can these extraordinary facts mean? Can they mean any thing, but that these three systems are reciprocally connected? A *suspicion* to this effect has been expressed by Milne-Edwards and M. Quatrefages; but the author claims the merit of having first produced demonstrative facts which impart to this suspicion a very probable character. The question admits of more confident answer in the higher genera. The blood-vessel of the *Sipuncle* may be readily exposed: it lies on the intestine in form a bright pink thread (fig. 10, *m, j*); it exists only on one side; it has no discoverable correlate on the opposed side of the cylinder; it is filled with pink fluid, the corpuscles of which are identical *un-*

* *Op. cit.* p. 127.

questionably with those floating on the fluid of the peritoneal cavity. The vessel may be readily isolated and placed detachedly under the eye of the microscope. The blood-corpuscles while in the vessel continue in ceaseless motion; this motion instantly ceases upon their escape from the vessel. Vibratile cilia may be actually *seen* on the internal lining membrane of the vessel: the motion is due to *their* vibration. Müller and Quatrefages and Dr. Peters incidentally refer to this phænomenon; by neither of these observers has it been referred to its true cause. In *no* other class of animals are the *internal* surfaces of true blood-vessels lined with cilia; it is because in the Echinoderms the blood-system is rudimentarily formed, that this aberrant phænomenon is intelligible. It is in the Echinoderms that the blood-proper system *first appears* in the zoological series. Nature's first effort is imperfect; the system is *not* independent of, closed off from, the other fluid systems of the organism; it derives its contents from those of the visceral cavity. The *water-vascular system* is exclusively locomotive and suctorial in function; it nowhere exhibits connexion with the branchial organs. Its fluid contents however indubitably communicate in some manner with those of the peritoneal cavity; the microscope *proves* them to be identical. In the Holothuridan genera these admit of more complete solution. In them the *three* systems exist under a pronounced form. The blood-system is more highly developed than in the inferior Echinoderms; it supplies branches to the tentacles, to the integuments, and forms a mesenteric plexus. The cavity of the body is notwithstanding filled by a highly corpusculated fluid, which penetrates into the hollow of the tentacles, and comes into near contact with the surrounding element through the *fenestræ* of the integument. In this genus then the *two* fluid systems are *separately* submitted to the process of aëration. The *parietes* of the tentacles bear a ramification of true blood-vessels. Their hollow axes are filled with chylaqueous fluid. But in the Holothuridæ a *fourth* system of fluids is superadded—that of the respiratory tree. The meaning of the respiratory tree is even now enigmatical; it consists of a cæcal, subdivided tube, filled with sea water, and communicating openly with the cloaca. *It floats in the fluid of the visceral cavity.* Its parietes are *not* supplied by a plexiform vascular system. The plexus formed by the blood-vessels lies in the folds of the mesentery, and belongs to the intestine; it exhibits no connexion with the *respiratory tree.* What then can be the signification of this excentric and paradoxical organ? Every comparative physiologist from Tiedemann to Müller has recognised in it a true respiratory organ; but in what possible manner can it accomplish such a function? The sea water admitted into its interior cannot affect the true blood; its parietes are *not* supplied by blood-bearing plexuses. The latter are remotely situated. To what uses then is it dedicated? It is surrounded by, it floats in the mass of the chylaqueous fluid. From their relative positions, it is manifest that the fresh sea water admitted into the respiratory tree *either itself, or the air by which it is charged,* passes by endosmose through the partition of the parietes, and that the chylaqueous fluid in the closed visceral cavity, *either itself,* or the effete gases by which it becomes impregnated, passes out *into* the respiratory tree by exosmose. *This* is the real function of the "respiratory tree of the *Holothuria.*" It is an excentric apparatus artfully provided, to renovate the composition and replenish the volume of the chylaqueous fluid. Thus is presented a summary statement of the *mechanism* of respiration in the Echinoderms.

EXPLANATION OF PLATE XII.

Fig. 1. Plan in outline of an Asteroid Zoophyte: *a* & *d*, visceral cavity or space between stomach and exterior of the body in which the chylaqueous fluid is contained; *b*. shows the mode in which the tentacles are supposed by some observers to terminate in and open into the stomach itself; *c*, orifice at the bottom of stomach.

Fig. 2. Plan of Hydraform Polype: *a*, base of tentacle opening into the perigastric areolæ *c*; *b*, stomach.

Fig. 3. Actiniform Polype: *b*, visceral cavity; *a*, orifice at bottom communicating with this cavity; *c*, tubular base of tentacle; *d*, *cilia* lining the interior of tentacle.

Fig. 4. Plan of a Bryozoon: *a*, base of tentacle communicating with the visceral cavity *b*.

Fig. 5. Plan of *Rhizostoma* (*Medusa*): *b*, digestive sac; *d*, *c*, gastro-vascular canal.

Fig. 6. Horizontal plan of the same: *a*, centre of digestive sac *b*; *c*, *d*, gastro-vascular canals.

Fig. 7. Vertical plan of a Ciliograde Medusan, *Pleurobranchus*: *c*, *d*, gastro-vascular canals.

Fig. 8. Section of an arm of *Asterias*: *a*, mouth; *e*, opening from mouth into the digestive cæcum *b*; *c*, its further cæcal end; *h*, cavity or body filled with the chylaqueous fluid; *f*, *f*, membranous tubular and *cæcal* processes (the true *branchiæ* of the Starfish).

Fig. 9. Vertical imaginary section of *Echinus*: *a*, mouth; *b*, anus; *d*, visceral cavity; *e*, intestine; *f*, *f*, *f*, hollow membranous processes—the true branchiæ of the *Echinus*; *g*, suctorial processes.

Fig. 10. Head and neck of Sipuncle: *B*, transverse section of one of the branchiæ, ciliated within and without; *C*, the same, viewed transparently; *i*, coiled intestine; *h*, corpuscles of chylaqueous fluid; *m*, *j*, blood-vessel; *n*, visceral cavity.

Fig. 11. A piece of the skin of Sipuncle showing the *branchial fenestræ* *d*, *d*, *d*: *a*, a pigmented *epidermal* cell in the centre of the *un*pigmented area *b*; *c*, pigmented cells of the intervals between the fenestræ.

[To be continued.]